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A CONTRIBUTION TO THE CYTOLOGY OF THE AUSTRALIAN-SOUTH PACIFIC SPECIES OF NICOTIANA*

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Although most of the fifty-eight species of the genus *Nicotiana* (Goodspeed[1]) are restricted to North and South America and adjacent islands, fifteen are peculiar to Australia and the South Seas. Of these, thirteen are limited to Australia, one, *N. Debneyi*, to Australia, New Caledonia and Lord Howe Island, and one, *N. fragrans*, occurs on the Isle of Pines near New Caledonia and eastward in a few scattered localities to the Marquesa Islands in the mid-South Pacific. As was recognized by Goodspeed,[2] the fifteen Australian-South Pacific species form a "genetic group" which he[1] has now designated as the section SUAVEOLENTES of the subgenus PETUNIOIDES. Its nearest relatives today are South American species of the ALATAE, ACUMINATAE and NOCTIFLORAE sections of that subgenus. The readiness with which morphological elements that give individuality to each of those three sections can be recognized in members of the SUAVEOLENTES suggests that all four sections may have been derived from a common source.

Detailed descriptions of species in the SUAVEOLENTES were given by the author[3] in 1935. The general pattern is that of an herb with conspicuous basal rosette or cushion of leaves and short, slender, forking stems terminating in long, spreading, loosely branching inflorescences. *N. suaveolens*, a variable species of medium flower size (25–45 mm. long) and obovate cauline leaf approximates the morphological mean. From it, *N. fragrans*, *N. Debneyi* and *N. Benthamiana* are the most extreme departures although only the last-named species is separated by any considerable hiatus unbridged by other species. *N. fragrans* has certain of the characters of *N. suaveolens* and also some of a long-flowered species, *N. megalosiphon*. *N. Debneyi* is approached by the small-flowered species, *N. exigua*, and in leaf and indument by *N. occidentalis*. In addition, *N. maritima* may be placed close to *N. velutina*, *N. suaveolens* and *N. Gossei*; *N. Gossei* to *N. excelsior*;

N. Goodspeedii to *N. exigua* and *N. rotundifolia*; *N. rotundifolia* to *N. occidentalis*. In other words, the section SUAVEOLENTES is an herbaceous group, the individual species of which appear to be complexly interrelated and in general separated by distinctions of only small magnitude. As a contribution to the cytology of this geographically isolated section and its interpretation, this study presents data on chromosome number and morphology in thirteen species and evidence bearing upon chromosome homology in twelve.

Chromosome Number.—According to Goodspeed[4] twenty-eight of the American species of *Nicotiana* are characterized by a somatic chromosome number of 12 pairs, nine species have 24 pairs, three have 9 pairs, two have 10 pairs. Among the Australian-South Pacific species there are no 9-, 10- or 12-paired ones but, as previously reported by Goodspeed and Clausen,[5] East (from Goodspeed),[6] Goodspeed (from Wheeler),[2,7] Kostoff, Dogadkina and Tichonova,[8] Wheeler,[3] Kostoff,[9,17] Kostoff (from Clausen),[9] there were four species which possess 16, three 18, two 20 and one each 22, 24 or 32† pairs. The author has now determined that two species, *N. Benthamiana* and *N. excelsior*, stated by Kostoff[9,17] to be 18-paired are 19 paired in her material, and in addition reports 21 pairs for *N. occidentalis* and 24 pairs for *N. fragrans*, species for which chromosome number had not previously been determined. Thus, as shown in table 1, the series begins with 16 pairs, closes with 24 and lacks only 17- and 23-paired species of being continuous. It is composed of four species with 16 pairs (one containing 32-paired races†), one with 18, two with 19, two with 20, one with 21, one with 22 and two with 24. The species which is selected as the morphological mean, *N. suaveolens*, has 16 pairs. *N. fragrans* and *N. Debneyi*, outstanding variants in the group, have 24 pairs. The species of greatest morphological isolation, *N. Benthamiana*, has 19 pairs. Identity or similarity in chromosome number may or may not parallel similarity in external morphology. In the case of three of the 16-paired species, of an 18-paired and one of the 19-paired (*N. excelsior*), and of a 21- and 22-paired, it does. By contrast, the lack of correlation is striking in the two 20-paired and the two 24-paired species.

Chromosome Morphology.—The only comprehensive work on karyotypes in the American species of *Nicotiana* is that of Goodspeed.[7,4] Those species have an average chromosome length of from 2.2 μ in the genom of shortest chromosomes to at least 5.5 μ in the genom of longest chromosomes. Three categories of chromosomes are recognized: median ("*x*") chromosomes in which the centromere position is median, submedian ("*sm*") chromosomes where it is nearer the middle than the end, and subterminal ("*st*") chromosomes where it is as near to the end as to the middle or nearer. Some species show only *m* or *sm* chromosomes, most have more *m* and *sm* than *st* chromosomes, and four (two each of sections

NOCTIFLORAE and ALATAE in the subgenus PETUNIOIDES) have exclusively *st* chromosomes. Satellites occur on at least one pair in each species, on two pairs in some, and rarely, in certain 24-paired species, on three pairs. In *N. Langsdorffii* there is an exceptionally large satellite. Constrictions not associated with centromere or satellite occur in some species.

For the Australian-South Pacific species partial analyses of the somatic complements of five species were reported by the author[12] and referred to by Goodspeed.[7] This earlier work was based upon paraffin sections of root tips. The complete and detailed analyses of chromosome morphology in table 1 of thirteen species of the section SUAVEOLENTES are products of recent studies in aceto-carmine smears of first microspore mitoses. For comparison with the rest of the genus the chromosomes are classified as to centromere position according to the terminology adopted by Goodspeed.

The length of the longest chromosome in its fully expanded condition in the SUAVEOLENTES is approximately 5 μ while the shortest is less than 2 μ. From species to species average chromosome length tends to decrease as number of chromosomes increases. Within a particular complement the longest chromosome usually is approximately twice the length of the shortest although in *N. Benthamiana*, *N. Debneyi* and *N. fragrans* the distinction is much less; the transition from longest to shortest is gradual.

As shown in table 1 there is no Australian-South Pacific species which possesses either all *m* or *sm* chromosomes or all *st* chromosomes. The lowest per cent of *st* (25%) occurs in the 16-paired species, *N. suaveolens*, *N. maritima* and *N. velutina*, the highest (79%) in the 24-paired species, *N. Debneyi*. In the main, as number of chromosomes in the complement increases there is progressive increase in number of *st* at the expense of *m* and *sm* chromosomes, but the relation is not a perfect one. *N. fragrans*, a 24-paired species, shows only 67 per cent of *st* and *N. Benthamiana*, a 19-paired, 74 per cent. Throughout, a proximal satellite occurs either on one pair of *st* chromosomes or on a pair which is almost on the border line between an *sm* and an *st* centromere position. In *N. fragrans* two pairs with proximal satellites apparently occur. Another satellite, in some species on the shorter arm of an *sm* chromosome and in others on an *m* chromosome, has been demonstrated in eleven species. It may also occur in *N. occidentalis* but the evidence is not conclusive. In *N. Benthamiana* a large segment separated by a distinct thread and peculiar to an *sm* chromosome is conspicuous. It is a question whether it has replaced the satellite mentioned and, if so, whether it is characteristic of all races of the species. In appearance it approximates the large satellite found in *N. Langsdorffii* of the ALATAE section (cf. Goodspeed[7]). Possibly more than two satellites will be found in *N. Debneyi;* there are six nucleoli in this species. On one to four *m* or *sm* chromosomes of all species except *N. Benthamiana* an additional slight constriction has been noted. When

most clearly shown, the chromosome arm containing it appears segmented, although in other cases a flexure may be the only indication.

In general it may be said of the karyotypes of the Australian-South Pacific species of *Nicotiana* that: (1) They show no morphological feature not also present elsewhere in the genus and particularly in those PETUNIOIDES

TABLE 1

CHROMOSOME MORPHOLOGY

SPECIES	TOTAL PAIRS	*m* PAIRS	*sm* PAIRS	*st* PAIRS
N. suaveolens Lehm.	16	8 (1s)	4 (1s)	4
N. maritima Wheel.	16	8 (1s)	4 (1s)	4
N. velutina Wheel.	16	8 (1s)	4	4 (1s)
N. exigua Wheel.	16	6 (1s)	5	5 (1s)
N. Gossei Domin	18	5	4 (1s)	9 (1s)
N. excelsior Black	19	5	4 (1s)	10 (1s)
N. Benthamiana Domin	19	1	4 (1s?)	14 (1s)
N. megalosiphon Heurck and Muell. Arg.	20	2	4 (1s)	14 (1s)
N. Goodspeedii Wheel.	20	6 (1s)	4 (1s)	10
N. occidentalis Wheel.	21	4	3	14 (1s)
N. rotundifolia Lindl.	22	4 (1s)	3	15 (1s)
N. Debneyi Domin	24	4 (1s)	1	19 (1s)
N. fragrans Hook.	24	2 (1s)	6	16 (2s?)

m, centromere median; *sm*, submedian; *st*, subterminal. 1s, a satellite on one pair

sections of closest resemblance (cf. Goodspeed[4]). (2) While no single karyotype pattern obtains consistently throughout the section save that all complements have *m*, *sm* and *st* chromosomes, nevertheless there is unity, for there is no complement that cannot be related morphologically in some degree to that of every other species and, usually, related closely to that of one or more species. In this respect, chromosome morphology sometimes gives better indication of degree of relationship than chromosome number alone. A case in point is the closer relationship of *N. Gossei* (18 pairs) to *N. excelsior* (19) than of either species to *N. Benthamiana* (19). (3) If one wishes to consider the section that in the light of Lewitsky's[13] hypothesis that complements of equal-sized, equal-armed chromosomes usually are the more primitive (cf. also Sarana,[14] Goodspeed[15]), phyletically the SUAVEOLENTES appear to be one of the more specialized groups in the genus and to have proceeded a long distance from the condition described by Goodspeed for the PANICULATAE section of the subgenus RUSTICA. However, no individual species of the SUAVEOLENTES has a complement consisting entirely of unequal-armed chromosomes. Hence, according to Lewitsky's hypothesis, no SUAVEOLENTES species has reached the degree of arm length specialization possible for its chromosome number which *N. longiflora* of the ALATAE section as described by Hollingshead[16] has attained.

Chromosome Homology.—Chromosome association to form bivalents or higher valencies at the first meiotic metaphase is considered here to be evidence of homology, i.e., evidence of a high degree of genic and structural similarity of entire chromosomes or of sufficiently large segments thereof to favor chiasmata formation. Non-homologous association may occur but its incidence is assumed to be negligible. In what follows, therefore, homology is discussed in terms of pairing.

Chiefly Kostoff[17,9] and Goodspeed[7,15] have studied the cytology of thirty-eight F_1 hybrids between Australian-South Pacific and American species. Evidence of a high degree of genic or structural distinction between the species involved in any given hybrid is indicated by the fact that in every case, except five involving a 32-paired race, pairing at MI is largely lacking. This also shows that in the complements of the SUAVEOLENTES species concerned, *N. suaveolens*, *N. maritima*, *N. exigua*, *N. Gossei*, *N. megalosiphon* and *N. Debneyi*, there is either little or no autosyndetic pairing.

Six interspecific F_1 hybrids between species of the SUAVEOLENTES were early examined cytologically by the author[12] but the first complete MI analyses of such intrasectional hybrids were published by Kostoff.[17,9] Exclusive of those in which a 32-paired race was a parent, he reported on the extent and quality of pairing in thirteen combinations. More recently the author has examined ten of the same and also investigated an additional sixteen hybrids. As far as it is possible to compare the data there is similarity between Kostoff's results and those listed in tables 2 and 3.

In the following tables when the parents differ in chromosome number the species of the lower number is placed first, irrespective of the direction in which the cross was made. Only pollen mother cells were studied and the amount and nature of chromosome association is reported on the basis of the first ten MI configurations which were completely analyzable in side view. Ten complete analyses were considered adequate for the purpose since studies of several times that number of pollen mother cells in a series of representative hybrids did not significantly alter the original conclusions. For example, where more than one "most frequent association" is recorded for ten counts, a sharply defined mode was not obtained with additional counts.

The above tables indicate that trivalents were seen in all but three of the twenty-six hybrids investigated. In more than half of them the most frequently observed association involved a trivalent and in two hybrids every pollen mother cell analyzed contained at least one valency higher than two. The occurrence of quadrivalents is less than that of trivalents, but one or more occurred within ten counts in thirteen hybrids. In a subsequent publication the incidence of all the types of chromosome association will be discussed in detail. Here only a summary of the some-

what complex situation concerned has been attempted. Column 2 gives the range of bivalents observed, column 3 the range in number of pairs calculated on the basis that one trivalent is equivalent to one pair and one quadrivalent to two pairs (cf. Goodspeed[15]), and column 4 the most frequent number of pairs in terms of a similar calculation. In column 4 the derivation of the number of pairs is shown by the number of trivalents in parentheses. For example, in F_1 *N. maritima* × *N. velutina* the "most

TABLE 2

CHROMOSOME ASSOCIATIONS AT MI IN F_1 HYBRIDS WHICH INVOLVE 16-PAIRED SPECIES

PARENTAL SPECIES	RANGE OF OBSERVED BIVALENTS	RANGE OF ASSOCIATIONS EXPRESSED AS BIVALENTS[a]	MOST FREQUENT ASSOCIATIONS EXPRESSED AS BIVALENTS[a]
16 × 16			
[K]*N. maritima—N. suaveolens*	16	16	16
[K]*N. maritima—N. velutina*	7–14	12–15 (1–5_{III}[b])	14 (2_{III})
[K]*N. velutina—N. exigua*	9–14	12–15 (0–$2_{III}1_{IV}$)	14 (1_{III})
[K]*N. velutina—N. suaveolens*	11–15	13–15 (0–2_{III}[b])	14
16 × 18			
[K]*N. maritima—N. Gossei*	12–16	14–16 (0–$1_{III}1_{IV}$)	15 (1_{III})
N. velutina—N. Gossei	12–15	13–16 (0–$1_{III}1_{IV}$)	15
[K]*N. suaveolens—N. Gossei*	13–15	13–15 (0–1_{IV})	15 (1_{III})
N. exigua—N. Gossei	10–14	13–15 (1–4_{III}[b])	14 (2_{III})
16 × 19			
N. suaveolens—N. Benthamiana	7–14	8–14 (0–1_{III})	8; 10; 11; 12 (0–1_{III})
16 × 20			
N. suaveolens—N. Goodspeedii	14–17	16–17 (0–2_{III}[b])	16 (1_{III}); 17
N. exigua—N. Goodspeedii	11–16	14–16 (0–$1_{III}1_{IV}$)	14 (2_{III}); 15 (1_{III})
[K]*N. suaveolens—N. megalosiphon*	9–15	10–15 (0–1_{III})	13 (0–1_{III}); 15 (1_{III})
[K]*N. exigua—N. megalosiphon*	10–14	10–14 (0–1_{III})	13; 14
N. velutina—N. megalosiphon	7–13	8–14 (0–1_{III})	12 (1_{III})
16 × 22			
N. velutina—N. rotundifolia	13–16	13–16	15; 16
16 × 24			
[K]*N. maritima—N. Debneyi*	11–16	14–16 (0–3_{III})	16 (3_{III})

[K], Kostoff also reports this cross.

[a] Univalents omitted.

[b] Quadrivalents occur in this hybrid but do not increase the range.

frequent association" is stated to be "14_{II} (2_{III})." This indicates that pollen mother cells containing $12\ _{II} + 2_{III} + 2_I$ were most often found. In column 3, although the range in number of pairs also is a product of translation of multivalents into pairs, the figures in parentheses express only the range of occurrence of trivalents and quadrivalents or combination of the two.

Exclusive of hybrids in which *N. Benthamiana*, *N. megalosiphon* and *N. occidentalis* are parents, it can be seen in tables 2 and 3 that the number of pairs is or approaches 16 if both parental species are 16-paired, or ap-

proximates that of the parental species possessing the smaller chromosome number if the two parents differ from each other in chromosome number (i.e., "Drosera scheme" association). Thus nine of the twelve species of the SUAVEOLENTES investigated exhibit a high degree of homology and thereby demonstrate concretely common origin even in instances of considerable divergence of chromosome number and chromosome morphology.

The hybrids which involve *N. Benthamiana* show the greatest range of pairs (6 to 15), the lowest mode when a mode occurs (11 pairs), and the

TABLE 3

CHROMOSOME ASSOCIATIONS AT MI IN F_1 HYBRIDS WHICH INVOLVE 18- TO 24-PAIRED SPECIES ONLY

PARENTAL SPECIES	RANGE OF OBSERVED BIVALENTS	RANGE OF ASSOCIATIONS EXPRESSED AS BIVALENTS[a]	MOST FREQUENT ASSOCIATIONS EXPRESSED AS BIVALENTS[a]
18 × 19			
N. Gossei—*N. excelsior*	16–18	17–18 (0–1_{III})	17 (1_{III}); 18
N. Gossei—*N. Benthamiana*	9–14	9–15 (0–1_{III})	11 (1_{III})
18 × 20			
[K]*N. Gossei*—*N. megalosiphon*	11–16	13–17 (0–$1_{III}1_{IV}$)	15 (1_{III})
18 × 21			
N. Gossei—*N. occidentalis*	11–14	13–15 (0–2_{III}[b])	14
19 × 20			
N. Benthamiana—*N. megalosiphon*	6–14	6–15 (0–1_{III})	6; 10; 14 (0–1_{III}).
19 × 24			
N. Benthamiana—*N. Debneyi*	9–16	9–17 (0–$1_{III}1_{IV}$)	11
20 × 20			
N. Goodspeedii—*N. megalosiphon*	12–16	12–16	13; 15
20 × 22			
N. Goodspeedii—*N. rotundifolia*	17–20	17–20 (0–2_{III})	19 (1–2_{III})
20 × 24			
N. Goodspeedii—*N. Debneyi*	15–19	16–20 (0–2_{III}[b])	19 (1_{III})
N. megalosiphon—*N. Debneyi*	9–15	9–16 (0–1_{III})	11; 14

[K], Kostoff also reports this cross.

[a] Univalents omitted.

[b] Quadrivalents occur in this hybrid but do not increase the range.

least tendency to form a mode. Those of *N. megalosiphon* and the one *N. occidentalis* hybrid may exhibit some or all of these characteristics, but to lesser degree. However, in hybrids with any of these three species as one of the parents, the range of calculated pairs reaches or approaches 16. Thus extent of pairing here also, indicates both considerable homology between these species and other Australian species and, possibly, some significance in the number 16.

The consistent formation of one or a few trivalents and an occasional quadrivalent in many Australian hybrids may be explained on the basis of translocation or duplication, as Kostoff[17] has suggested. Aside from 32-paired races of *N. suaveolens*, a special problem, Kostoff[17] submits certain

evidence of one large duplication in *N. megalosiphon*. The author's counts of F_1 *N. Goodspeedii* × *N. suaveolens* suggest a similar possibility in *N. Goodspeedii*. However both instances require further investigation before it can be said that this is true of either *N. megalosiphon* or *N. Goodspeedii* as a species. The most probable explanation of multivalency in many Australian hybrids is that translocation is involved.

Conclusion.—The somewhat specialized character of the Australian-South Pacific species, the general similarity in external morphology from species to species, and the apparent intricacy of interrelationships among them, are reflected in their cytology. Closer relationship between certain species and a more distant one in the case of others is indicated sometimes by chromosome number or morphology, sometimes only by chromosome behavior in hybrids. The following brief phyletic hypothesis is offered here as one possible interpretation of the facts presented: The 16-paired species are amphidiploid hybrids of 8-paired species. Although no 8-paired *Nicotiana* species are known today, postulation of their existence in past time is not unreasonable; species of 9 and 10 pairs, respectively, constitute the ALATAE, a related section of *Nicotiana* and in *Petunia*, a genus which borders closely upon the same section, there are 7- and 9-paired species. The 24-paired Australian-South Pacific species are derived from hybridization of 16-paired species with 8-paired (not necessarily the same 8-paired species in each case), followed again by amphidiploidy. Either a still higher level of hybridization, namely, 24-paired species with 16-paired, followed by selfing or backcrossing, but more readily by the latter, is responsible for initiation of a series of numbers between these two extremes, or possibly in the course of hybridization of 16-paired with 8-paired species sesquidiploidy (cf. Webber[18]) has thus functioned.

It is intended that papers published elsewhere will treat in greater detail of the external morphology, geographical distribution, chromosome morphology, and hybrid behavior in the SUAVEOLENTES. Hypotheses bearing upon the phylesis of these species will be more critically examined at that time.

Summary.—The fifteen Australian-South Pacific species of *Nicotiana*, or the SUAVEOLENTES section of the subgenus PETUNIOIDES, are a geographically isolated group of complexly interrelated herbaceous species, the specific differences of which generally are of small magnitude. Thirteen have been studied cytologically. Four 16-paired species, one 18-, two 19-, two 20-, one 21-, one 22- and two 24-paired occur. Usually a number of chromosomes with subterminal centromere increases at the expense of those with median or submedian, as chromosome number increases. Twenty-six hybrids involving twelve species show that considerable to high pairing between species obtains throughout in first meiotic metaphase. This indicates a common origin. A phyletic cytological hypothesis

involving a base number of 8 and repeated hybridization in part accompanied by chromosome doubling is offered as a possible interpretation of chromosome number, morphology and behavior in the SUAVEOLENTES.

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† Kostoff[10,11] has given a 32-paired race which he has grown the designation "*N. Eastii.*" The author does not consider this and another 32-paired race sufficiently distinct from *N. suaveolens* morphologically to warrant separation.

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ON A CLASS OF HERMITIAN TRANSFORMATIONS CONTAINING SELF-ADJOINT DIFFERENTIAL OPERATORS

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1. We consider the space $\mathfrak{L}_2(\Delta)$, that is, the space of all real and complex functions $f(x)$ defined in a certain (finite or infinite) closed interval Δ of the x-axis and such that $|f(x)|^2$ is Lebesque-integrable in Δ. The scalar product is then given by the relation

$$(f, g) = \int_\Delta f(x)\overline{g(x)}\,dx.$$

We denote by s any interior point of Δ, and introduce a family of projectors P_s in $\mathfrak{L}_2(\Delta)$ by writing

$$P_s f(x) = \begin{cases} f(x) & \text{for } x \leq s \\ 0 & \text{for } x > s \end{cases} \quad (x \in \Delta).$$

Now let H be a closed Hermitian transformation with domain $\mathfrak{D}$ contained in $\mathfrak{L}_2(\Delta)$, and denote by $\mathfrak{D}_s (\mathfrak{D}_s \subset \mathfrak{D})$ the set of all $f(x)$, such that both $f(x)$ and $P_s f(x)$ are elements of $\mathfrak{D}$. Clearly $\mathfrak{D}_s$ as well as $\mathfrak{D}$ is a linear manifold in $\mathfrak{L}_2(\Delta)$. If, moreover, $\mathfrak{D}_s$ is everywhere dense in $\mathfrak{D}$, then there exists a contraction ${}^sH$ of H with domain $\mathfrak{D}_s$. We further write as usual H^* for the adjoint of H, $H_\lambda = H - \lambda 1$, and $H_\lambda^* = H^* - \lambda 1$.

2. In this Note we are concerned with the class of Hermitian transformations H in $\mathfrak{L}_2(\Delta)$ satisfying the following conditions:

(α) *H is a closed Hermitian transformation*[1] *of deficiency index (m, m) with domain $\mathfrak{D}$.*

(β) *If $\{\varphi_\mu\}$ and $\{\psi_\mu\}$ are two sets of m linearly independent eigen solutions of H^* corresponding to the eigen values i and $-i$, respectively, so that $H_i^*\varphi_\mu = 0, H_{-i}^*\psi_\mu = 0, (\mu = 1, 2, \ldots, m)$, then the two sets of m elements $\{(P_t - P_s)\varphi_\mu\}$ and $\{(P_t - P_s)\psi_\mu\}$ are both linearly independent for every pair of numbers $s \neq t$ of Δ.*

(γ) *For every s interior to Δ, $\mathfrak{D}_s$ is everywhere dense in $\mathfrak{D}$; the contraction ${}^sH$ of H is of deficiency-index $(2m, 2m)$.*

(δ) *P_s and ${}^sH$ are commutative, so that for every f of $\mathfrak{D}_s$*

$${}^sHP_s f = P_s {}^sHf.$$

Such a transformation will be called an m^{th} order transformation of class P.

3. MAIN THEOREM. *Let H be an m^{th} order transformation of class P in $\mathfrak{L}_2(\Delta)$. If H satisfies the two additional conditions:*

(ϵ) *The differential quotients up to the m^{th} order of the m eigen solutions $\varphi_\mu = \varphi_\mu(x)$ defined in (β) exist at every point x of Δ,* and the $\psi_\mu = \psi_\mu \alpha$ are continuous in Δ.

(ζ) *$\mathfrak{D}_s \cdot \mathfrak{D}_t$ is everywhere dense in $\mathfrak{D}$ for every pair of numbers s, t contained in the interior of Δ.*

Then H^* can be represented by a self-adjoint differential operator[2] *of m^{th} order.*

Remark.—It is nearly obvious that the converse of the Theorem is true, i.e., that if H^* is an m^{th} order self-adjoint differential operator defined, in Δ, then its adjoint H satisfies the conditions (α) to (ζ).

The proof of this theorem will be given in a later paper. It is based entirely on the methods developed in [1] and [2], Chapter I.

4. There exist m^{th} order transformations of class P other than the self-

adjoint differential operators, which, naturally, cannot satisfy both of the conditions (ϵ) and (ζ). The later paper will give a method of obtaining all transformations of class P, and of representing them by means of certain integral equations.

We consider in particular the subclass $\mathfrak{S}_m$ of all those m^{th} order transformations H of class P whose m eigen solutions $\varphi_\mu(x)$, as defined in (β), have differential quotients up to the order $2m$ at every point x of Δ. (Hence the transformations of $\mathfrak{S}_m$ satisfy (α) to (ϵ) but not (ζ).) Let $\sigma(x)$ be any real, m-times differentiable function, $\sigma \equiv 0$ included, let $L_m(f)$ and $D_n(f)$ denote linear differential operators of order m and n, respectively ($n \leq m - 1$), and L_m^* and D_n^* Lagrange's adjoint operators. Then we can state the following:

THEOREM. *The subclass $\mathfrak{S}_m$ coincides with the class of all H, such that for all m-times differentiable functions $g(x)$ the relation $H_\lambda^* f = g$ can be represented in the form*[3]

$$L_m((\cos\sigma - \lambda\sin\sigma)f) - D_n((\sin\sigma + \lambda\cos\sigma)f) = L_m(g\sin\sigma) + D_n(g\cos\sigma) \tag{1}$$

subject to the following three conditions for L_m, D_n and σ:

(i) *The linear operator $L_m D_n^*$ of order $m + n$ is self-adjoint.*

(ii) *The differential equation*

$$L_m((\cos\sigma - i\sin\sigma)y) - D_n((\sin\sigma + i\cos\sigma)y) = 0$$

has a fundamental system of m solutions $\varphi_\mu(x)$ which are all elements of $\mathfrak{L}_2(\Delta)$.

(iii) *The differential equation*

$$L_m(z\sin\sigma) + D_n(z\cos\sigma) = 0$$

has singularities at both end-points of Δ, such that there exists no particular integral z of it for which $|z|^2$ is Lebesque-integrable in any sub-interval of Δ containing at least one of the end-points of Δ.

It can readily be shown that transformations of the subclass $\mathfrak{S}_m$ exist for all m, with $\sigma(x) \equiv 0$ as well as with $\sigma(x) \not\equiv 0$ in Δ. If $m \geq 2$, we can choose $n \neq 0$.

5. If we wish to obtain all real transformations of the subclass $\mathfrak{S}_m$ defined in **4** we only have to take those transformations defined by (1) where the operators L_m and D_n are both real. Then owing to condition (i) of the above Theorem, $m - n$ is even. Hence for $m = 2$ the transformations defined by

$$L_2((\cos\sigma - \lambda\sin\sigma)f) - (\sin\sigma + \lambda\cos\sigma)f = L_2(g\sin\sigma) + g\cos\sigma,$$

L_2 being a self-adjoint differential operator, are the only real transformations of the subclass $\mathfrak{S}_2$. If $\sigma \equiv 0$, we obtain the case of the Main-Theorem, $L_2(f) - \lambda f = g$.

6. In order to include the singular case dealt with first in a series of papers by H. Weyl[4] where the number of linearly independent solutions of $L_m(y) = \lambda y$, (λ non-real), belonging to $\mathfrak{L}_2(\Delta)$ is less than the order of $L_m(y)$, we introduce the following generalization of the transformations of class P:

Definition.—Let Δ' be any interval $a' \leqslant x \leqslant b'$ whose end-points a' and b' are interior points of Δ, and write $P_\Delta' = P_{b'} - P_{a'}$. Then H, with domain $\mathfrak{D}$ in $\mathfrak{L}_2(\Delta)$, is an m^{th} order transformation of the generalized class P, if $P_\Delta' H P_\Delta'$ with domain $\mathfrak{D} \cdot \mathfrak{L}_2(\Delta')$ is an m^{th} order transformation[5] of class P in $\mathfrak{L}_2(\Delta')$ for every Δ'. This definition implies, firstly, that $P_\Delta' H P_\Delta'$ satisfies condition (ζ) for every Δ' and every pair of points s, t contained in Δ', and, secondly, that there exists a set of m linearly independent functions $\varphi_\mu(x)$ defined in every interior point x of Δ such that for every Δ'

$$P_\Delta' \varphi_\mu \in \mathfrak{L}_2(\Delta'), \quad (P_\Delta' H_i P_\Delta')^* \varphi_\mu = 0 \quad (\mu = 1, 2, \ldots, m). \tag{2}$$

Hence the Main Theorem of **3** in the generalized case takes the following form:

THEOREM. *If H is an m^{th} order transformation of the generalized class P in $\mathfrak{L}_2(\Delta)$, and if the functions $\varphi_\mu(x)$ defined in (2) satisfy condition (ϵ), then H^* can be represented by a self-adjoint differential operator of m^{th} order.*

7. Finally, we define a class P of Hermitian transformations H given in any abstract Hilbert space $\mathfrak{H}$. Let $P(s)$ be a resolution of the identity defined in $\mathfrak{H}$ for every point s of a (finite or infinite) interval Δ, such that

$$1 = \int_\Delta dP_{(s)}$$

Let the Hermitian operator K defined in $\mathfrak{H}$ by the relation

$$K = \int_\Delta s dP(s)$$

be such that (i) K has no eigen value, (ii) K has simple spectrum, and (iii) no point of Δ belongs to the resolvent set of K. Then a closed Hermitian transformation H in $\mathfrak{H}$ is an m^{th} order transformation of class P, if there exists any resolution of the identity $P(s)$ in $\mathfrak{H}$ with the properties (i), (ii) and (iii), with respect to which H satisfies conditions (α) to (δ).

In order to obtain a theorem for the class P in $\mathfrak{H}$ which corresponds to the Main Theorem for the class P in $\mathfrak{L}_2(\Delta)$, we consider the one-one mapping of $\mathfrak{H}$ on to $\mathfrak{L}_2(\Delta)$ carried out[6] by means of a suitable element g_0 of $\mathfrak{H}$ such that any element $f(x)$ of $\mathfrak{L}_2(\Delta)$ and the corresponding f of $\mathfrak{H}$ are connected by the relation

$$f = \int_\Delta f(s) d(P(s) g_0). \tag{3}$$

Then the Main Theorem takes the following form:

THEOREM. *Let H be an m^{th} order transformation of class P in $\mathfrak{H}$ which*

also satisfies condition (ζ), *and let* $\{\varphi_\mu\}$ *and* $\{\psi_\mu\}$ *be each a set of* m *linearly independent eigen solutions of* H^* *corresponding to the eigen values* i *and* $-i$, *respectively. If we can find a mapping of* $\mathfrak{H}$ *on to* $\mathfrak{L}_2(\Delta)$ *of the form* (3) *which maps the sets of elements* $\{\varphi_\mu\}$ *and* $\{\psi_\mu\}$ *on to sets of functions* $\{\varphi_\mu(x)\}$ *and* $\{\psi_\mu^{(x)}\}$ *satisfying condition* (ϵ), *then this mapping takes* H *into a self-adjoint differential operator of* m^{th} *order defined in* $\mathfrak{L}_2(\Delta)$.

In the same way the generalized class P of m^{th} order in $\mathfrak{L}_2(\Delta)$ can be extended to a generalized class P of m^{th} order in $\mathfrak{H}$. We omit the details.

[1] Hamburger, H. L., *Quart. Jour. Math.* (Oxford Series), **13**, 117–128 (1942).
[2] Hamburger, H. L., *Ann. Math.*, **45**, 59–99 (1944).
[3] Stone, M. H., *Linear transformations in Hilbert space*, New York, 1932.
[4] Weyl, H., *Math. Annalen*, **68**, 220–269 (1910).
[5] Weyl, H., *Göttinger Nachrichten*, pp. 442–467, 1910.

[1] See the definition of deficiency-index in [3] p. 81, Definition 2.21; p. 338, Definition 9.1.

[2] Here we use the word self-adjoint with the meaning which is implicit in Lagrange's general theory of ordinary linear differential equations. This differs essentially from its use in von Neumann's Theory (see [3], p. 50, Definition 2.11; p. 347, the last four lines), where a self-adjoint operator denotes a closed Hermitian operator of deficiency-index (0, 0).

[3] The equation (1) determines the relation $H_\lambda^* f = g$ only in a subdomain $\hat{\mathfrak{D}}$ of $\mathfrak{D}^*$, the domain of H^*. $\hat{\mathfrak{D}}$ is everywhere dense in $\mathfrak{D}^*$. If $\hat{H}_\lambda$ denotes the contraction of H_λ^* defined in $\hat{\mathfrak{D}}$, then it can be shown that $\hat{H}_\lambda$ is not closed, and that H_λ^* is the closure of $\hat{H}_\lambda$.

[4] See [4] and [5]; see also [3], pp. 458–498.

[5] If H, as a transformation in $\mathfrak{L}_2(\Delta)$, is itself of deficiency-index (m, m), then we are reduced to the case dealt with in **2** and **3**. In order to obtain something new, we have to assume that H in $\mathfrak{L}_2(\Delta)$ is of deficiency-index (m', m'), where $0 \leq m' < m$.

[6] See [3], p. 226, Theorem 6.2; pp. 275–277, Theorems 7.9 and 7.10.

NEW TYPES OF RELATIONS IN FINITE FIELD THEORY (SECOND PAPER)

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In the first paper published in these PROCEEDINGS under the above title,[1] the writer obtained some new types of relations in finite field theory. Here we shall proceed further along these general lines.

Mitchell[2] considered the relation

$$ax^m = by^m + 1 \qquad (1)$$

in a finite field of order p^{2n}, p prime, including the given coefficients a and

b, with $p^{2n} - 1 = mc$, and there exists an n_1 such that $p^{n_1} \equiv -1 \pmod{m}$ and $n = sn_1$. He found that if a and b were each mth powers in $F(p^{2n})$, then the number of solutions (x^m, y^m) of (1) in this case is

$$\frac{1}{m^2}(p^{2n} + (m-1)(m-2)(-1)^{s-1}p^n - 3m + 1). \tag{2}$$

Also if a is an mth power and b is not, or conversely, then the number of solutions (x^m, y^m) of (1) is

$$\frac{1}{m^2}(p^{2n} - (m-2)(-1)^{s-1}p^n - m + 1). \tag{3}$$

If neither a nor b nor a/b is an mth power in the field, he found the number of solutions to be

$$\frac{1}{m^2}(p^{2n} + 2(-1)^{s-1}p^n + 1). \tag{4}$$

We now modify the method employed by the writer in another paper[3] to obtain other relations involving the number of solutions of (1), and we find as in the proof of Theorem I of that paper that in the field $F(p^{2n})$ we have, if N is the number of solutions of (1), and if

$$h = \frac{t(p^n - 1)}{c}, \tag{4a}$$

then

$$N = -c^2 \sum_{k=1}^{h} \sum_{r=0}^{k} \binom{kc}{rc} a^{mc-kc} b^{rc}$$

in the field. Comparing this with (2), (3), and (4), we have, noting that $p = 0$ in $F(p^{2n})$, the

THEOREM I. *In a finite field of order p^{2n}, with $p^{2n} - 1 = mc$, and such that there exists an n_1 such that $p^{n_1} \equiv -1 \pmod{m}$ then, if h is defined as in (4a), the expression*

$$\sum_{k=1}^{h} \sum_{r=0}^{k} \binom{kc}{rc} a^{mc-kc} b^{rc}$$

equals $(3m-1)$, $(m-1)$ or -1 in $F(p^{2n})$ according as (1) a and b are each mth powers; (2) a is an mth power and b is not or conversely; (3) neither a nor b are mth powers, and also $a^c/b^c \neq 1$.

In another paper,[4] the writer obtained the results that if p belongs to the exponent n, modulo l, and $p^n = 1 + cl$, where p and l are odd primes and n is even, and if by definition

$$\binom{m}{n} = 0 \tag{4b}$$

where $n > m$, then

$$\sum_{t=0}^{\infty}\binom{c}{a+tl} \equiv 0 \pmod{p}$$

except when $2a \equiv c \pmod{l}$, in which case the right-hand member is unity. We shall here extend this relation by generalizing the argument employed for the original proof.

If $\zeta = e^{2i\pi/l}$ and $\mathfrak{p}$ is a prime ideal divisor of (p) in $k(\zeta)$, then, if $k \not\equiv 0 \pmod{l}$,

$$\left(\frac{1+\zeta^k}{\mathfrak{p}}\right) = \left(\frac{\zeta^{k/2}}{\mathfrak{p}}\right)\left(\frac{\zeta^{k/2}+\zeta^{-k/2}}{\mathfrak{p}}\right) \tag{5}$$

where these symbols represent power characters in $k(\zeta)$. Since

$$\left(\frac{\zeta^{k/2}+\zeta^{-k/2}}{\mathfrak{p}}\right) = 1,$$

(5) gives (6) and (7), for s an integer $\geqq 0$.

$$(1+\zeta^k)^{cs} \equiv \zeta^{cks/2} \pmod{\mathfrak{p}}. \tag{6}$$

$$(1+\zeta^k)^{cs+r} \equiv \zeta^{cks/2}(1+\zeta^k)^r \pmod{\mathfrak{p}},\ 0 \leqq r < c. \tag{7}$$

Since (7) holds for each value of $k \not\equiv 0 \pmod{l}$, we may expand and, after reducing each ζ^k by the relation $(\zeta^k)^l \equiv 1$, collect terms of the left- and right-hand members separately, calling the sum of the coefficients of $(\zeta^k)^i$ on the left A_i, and the sum of the coefficients of $(\zeta^k)^i$ on the right B_i. Transposition will give the following array, where each dth line is the special case for $k = d$, and each coefficient $(A_i - B_i)$ is abbreviated to K_i: $i = 0, 1, \ldots, l-1$.

$$\left.\begin{array}{llll}
K_0 + K_1 & + K_2 & + \ldots + K_{l-1} & \equiv 0 \\
K_0 + K_1(\zeta) & + K_2(\zeta)^2 & + \ldots + K_{l-1}(\zeta)^{l-1} & \equiv 0 \\
K_0 + K_1(\zeta^2) & + K_2(\zeta^2)^2 & + \ldots + K_{l-1}(\zeta^2)^{l-1} & \equiv 0 \\
\ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots \\
\ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots \\
K_0 + K_1(\zeta^{l-1}) & + K_2(\zeta^{l-1})^2 & + \ldots + K_{l-1}(\zeta^{l-1})^{l-1} & \equiv 0
\end{array}\right\} \tag{8}$$

modulo $\mathfrak{p}$. Consider the determinant formed by the coefficients K_i. It is an alternant which may be expressed, aside from powers of ζ, as the product of binomials of the type ζ^{q-1}, when $0 < q < l$. Any ideal $(\zeta^q - 1)$ is a prime ideal divisor of (l), hence is prime to (p). Therefore, $K_i = A_i - B_i \equiv 0 \pmod{p}$; $i = 0, 1, \ldots, l-1$. Substitution of the actual values of A_i and B_i, obtained by the binomial expansion, gives a formula which may be expressed in the form (9), provided we define

$$\binom{0}{0} = 1. \tag{8a}$$

$$\sum_{t=0}^{\infty} \binom{cs + r}{a + tl} \equiv \sum_{t=0}^{\infty} \binom{r}{u + tl} \pmod{p}, \tag{9}$$

where a and u are integers, such that $u \equiv a - \frac{cs}{2} \pmod{l}$, $0 \leqq u \leqq l$, and $0 \leqq a < l$.

Also when, as before, $k \not\equiv 0 \pmod{l}$, then

$$\left(\frac{1 - \zeta^k}{\mathfrak{p}}\right) = \left(\frac{\zeta^{k/2}}{\mathfrak{p}}\right)\left(\frac{\zeta^{k/2} - \zeta^{-k/2}}{\mathfrak{p}}\right). \tag{10}$$

Since

$$\left(\frac{\zeta^{k/2} - \zeta^{-k/2}}{\mathfrak{p}}\right) = 1,$$

(10) gives

$$(1 - \zeta^k)^{cs} \equiv \zeta^{cks/2} \pmod{\mathfrak{p}}. \tag{11}$$

Hence

$$(1 - \zeta^k)^{cs+r} \equiv \zeta^{cks/2} (1 - \zeta^k)^r \pmod{\mathfrak{p}}, \; 0 \leqq r < c. \tag{12}$$

Whence, as before, except that here $r > 0$,

$$\sum_{t=0}^{\infty}\left[(-1)^{a+tl}\binom{cs + r}{a + tl}\right] \equiv \sum_{t=0}^{\infty}\left[(-1)^{u+tl}\binom{r}{u + tl}\right] \pmod{p}, \tag{13}$$

where a and u are integers such that $u \equiv a - \frac{cs}{2} \pmod{l}$, $0 \leqq u < l$, and $0 \leqq a < l$. Where, however, $r = 0$, then since (11) holds for each value of $k \not\equiv 0 \pmod{l}$, we may expand the left-hand member and set up the following array, where each dth line is the special case for $k = d$, and where each A_i is the sum of the coefficients of $(\zeta^k)^i$, each ζ^k being reduced by the relation $(\zeta^k)^l \equiv 1$:

$$\left.\begin{array}{llllll}
A_0 + A_1 & + A_2 & + A_3 & + \ldots + A_{l-1} & \equiv 0, \\
A_0 + A_1\zeta & + A_2\zeta^2 & + A_3\zeta^3 & + \ldots + A_{l-1}\zeta^{l-1} & \equiv \zeta^{cs/2}, \\
A_0 + A_1(\zeta^2) & + A_2(\zeta^2)^2 & + A_3(\zeta^2)^3 & + \ldots + A_{l-1}(\zeta^2)^{l-1} & \equiv (\zeta^2)^{cs/2}, \\
\ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots \\
\ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots & \ldots\ldots \\
A_0 + A_1(\zeta^{l-1}) & + A_2(\zeta^{l-1})^2 & + A_3(\zeta^{l-1})^3 & + \ldots + A_{l-1}(\zeta^{l-1})^{l-1} & \equiv \\
 & & & & (\zeta^{l-1})^{cs/2},
\end{array}\right\} \tag{14}$$

modulo $\mathfrak{p}$. Adding these congruences gives

$$lA_0 \equiv -1 \pmod{p}, \text{ if } \frac{cs}{2} \not\equiv 0 \pmod{l}.$$

To determine, in general, the value of any A_i, multiply each dth row of the original array by $(\zeta^{d-1})^{-i}$. The addition of the congruences of the resulting array gives

$$lA_i \equiv -1 \pmod{p}, \text{ if } \frac{cs}{2} - i \not\equiv 0 \pmod{l}; \tag{15}$$

$$lA_i \equiv l - 1 \pmod{p}, \text{ if } \frac{cs}{2} - i \equiv 0 \pmod{l}. \tag{16}$$

The relations (9), (13), (15), and (16) give

THEOREM II. *If p belongs to the exponent n, modulo l, and $p^n = 1 + cl$, where p and l are odd primes and n is even, and if s is any integer > 0 and a and u are integers, such that*

$$u \equiv a - \frac{cs}{2} \pmod{l}, \ 0 \leqq u < l, \text{ and } 0 \leqq a < l,$$

then

$$\sum_{t=0}^{\infty} \binom{cs + r}{a + tl} \equiv \sum_{t=0}^{\infty} \binom{r}{u + tl} \pmod{p};$$

for r an integer $\geqq 0$;

$$\sum_{t=0}^{\infty} \left[(-1)^{a+tl} \binom{cs + r}{a + tl} \right] \equiv \sum_{t=0}^{\infty} \left[(-1)^{u+tl} \binom{r}{u + tl} \right] \pmod{p},$$

if r is an integer > 0;

$$l \left\{ \sum_{t=0}^{\infty} \left[(-1)^{a+tl} \binom{cs}{a + tl} \right] \right\} \equiv -1 \pmod{p},$$

if $cs/2 - a \not\equiv 0 \pmod{l}$
and

$$l \left\{ \sum_{t=0}^{\infty} \left[(-1)^{a+tl} \binom{cs}{a + tl} \right] \right\} \equiv l - 1 \pmod{p},$$

if $cs/2 - a \equiv 0 \pmod{l}$.

As an application of Theorem II, we shall now prove the following:

THEOREM III. *If F is a finite field containing b and of order $p^{2n} = 1 + cl$ (where p and l are odd primes) and if p belongs to the exponent $2n$ (modulo l) and $bxy \neq 0$, and where N denotes the number of solutions (x^c, y^l) in F of the equation*

$$x^c + by^l + 1 = 0, \tag{17}$$

then

$$N \equiv 1 \pmod{p}, \text{ if } (c, l) = 1; \tag{18}$$

$$N \equiv 0 \pmod{p}, \text{ if } (c, l) = l \text{ and } b^c \not\equiv 1 \pmod{p}; \tag{19}$$

$$N \equiv l \pmod{p}, \text{ if } (c, l) = l \text{ and } b^c \equiv 1 \pmod{p}. \tag{20}$$

By Theorem II of another paper,[5] for the equation (17)

$$N = -hi \sum_{k=1}^{l} \sum_{\rho=0}^{\gamma} \binom{ki}{h\rho} b^{p^{2n}-1-ki}(-1)^{ki},$$

where $h = l$, $i = c$, and $\gamma = [ki/h]$.

$$N = -lc \sum_{k=1}^{l} \sum_{\rho=0}^{\gamma} \binom{kc}{l\rho} b^{-kc}(-1)^{kc}. \tag{21}$$

Now $p^{2n} - 1$ is even and l is odd, so c is even. By application of Theorem II of this paper,

$$N \equiv \sum_{k=1}^{l} \sum_{\rho=0}^{\infty} \binom{0}{u + \rho l} b^{-kc} \pmod{p}, \tag{22}$$

where u is an integer, such that

$$0 \leqq u < l \text{ and } u \equiv -\frac{ck}{2} \pmod{l}.$$

Suppose $(c, l) = 1$. Then $u \not\equiv 0 \pmod{l}$, except when $k = l$, in which case $u = 0$, and we find, using (4b) and (8a), $N \equiv 1 \pmod{p}$.

Suppose $(c, l) = l$. Then $u = 0$ for every value of k, and (22) reduces to

$$N \equiv \sum_{k=1}^{l} b^{-kc} \pmod{p},$$

from which we obtain (19) and (20). This proves Theorem III.

In (17), x^c cannot take on more than l distinct values, and also we cannot have two solutions, (x^c, y_1^l) and (x^c, y_2^l), with $y_1^l \neq y_2^l$. Likewise, y^l cannot take on more than c distinct values, and for any two solutions, (x_1^c, y^l) and (x_2^c, y^l), $x_1^c = x_2^c$. Hence, the total number of solutions can never exceed either c or l, and (20) becomes $N = l$. In (19), $N = 0$, if either $c < p$ or $l < p$, and in (18), $N = 1$, if either $c < p + 1$ or $l < p + 1$.

[1] Vandiver, H. S., These PROCEEDINGS, **31**, 50–54 (1945).
[2] Mitchell, *Ann. Math.*, **18**, 120 (1917).
[3] These PROCEEDINGS, **30**, 362–367 (1944).
[4] *Ann. Math.*, (2), **28**, 330–332 (1927).
[5] These PROCEEDINGS, **31**, 170–175 (1945).

ON ALGEBRAIC LIE ALGEBRAS

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A subgroup A of the full linear group $GL(n, C)$ in n variables (C being the field of complex numbers) is called *algebraic* if the condition for a matrix σ of $GL(n, C)$ to belong to A can be expressed by a system of algebraic equations in the coefficients of σ. Clearly A is then a complex Lie group, and it is of interest to determine the Lie algebras which can be considered as Lie algebras of algebraic Lie groups. The question has been solved in a certain sense by Maurer;[1] here we propose to resume the study from a different point of view.

One of us[2] has defined the notion of a *replica* Y of a matrix X of degree n as any matrix Y which admits as its invariants all the tensor-invariants of X (where, in defining tensor-invariants, X is meant to be the symbol of an infinitesimal, not a finite, transformation; thus the vector invariants are the vectors $\mathfrak{x}$ such that $X\mathfrak{x} = 0$, and not $X\mathfrak{x} = \mathfrak{x}$. Now, let K be a field of characteristic 0 and let $\mathfrak{gl}(n, K)$ be the Lie algebra of matrices of degree n with coefficients in K. A subalgebra $\mathfrak{g}$ of $\mathfrak{gl}(n, K)$ will be called *algebraic* if every replica of a matrix $X \in \mathfrak{g}$ still belongs to $\mathfrak{g}$.

If K is the field C of complex numbers, it is easily seen that the Lie algebra spanned by all the replicas of a matrix X is the Lie algebra of the smallest algebraic subgroup of $GL(n, C)$ to contain the one-parameter group generated by X. It follows immediately that the Lie algebra of an algebraic group of matrices is algebraic. The converse is true and can be seen from the following considerations. Let $\mathfrak{g}$ be an algebraic Lie algebra; then we may consider the elements of $\mathfrak{g}$ as operating on a certain vector space $\mathfrak{M}$, and therefore also on the tensor spaces $\mathfrak{T}_{r,s}$ which can be constructed on $\mathfrak{M}$ ($\mathfrak{T}_{r,s}$ is the space of r times contravariant and s times covariant tensors). Now we consider all pairs of vector subspaces $(\mathfrak{P}, \mathfrak{Q})$ of all $\mathfrak{T}_{r,s}$ such that $\mathfrak{Q} \subset \mathfrak{P}$, $X_{r,s}(\mathfrak{P}) \subset \mathfrak{Q}$ for all $X \in \mathfrak{g}$ (where $X_{r,s}$ is the operation on $\mathfrak{T}_{r,s}$ which corresponds to X). It can then be proved that if a matrix X' is such that $X'_{r,s}(\mathfrak{P}) \subset \mathfrak{Q}$, then X' belongs to $\mathfrak{g}$. It is clear that a condition of the form $X'_{r,s}(\mathfrak{P}) \subset \mathfrak{Q}$ can be expressed by algebraic equations on the coefficients of the matrices of the one-parameter group generated by X'. It then follows that *any algebraic Lie algebra over the field of complex numbers is the Lie algebra of an algebraic group of matrices.* Moreover, our method of proof gives an indication as to how to write down a system of finite equations which define the group.

Let $\mathfrak{g}$ be any subalgebra of $\mathfrak{gl}(n, K)$. Among all the algebraic Lie algebras to contain $\mathfrak{g}$, there clearly exists a smallest one, say $\mathfrak{g}^*$. It can be proved

that $\mathfrak{g}^*$ has the same derived algebra as $\mathfrak{g}$ itself and that every ideal in $\mathfrak{g}$ is also an ideal in $\mathfrak{g}^*$.

Let $\mathfrak{g}$ be any algebraic Lie algebra. Denote by $\mathfrak{h}$ the radical of $\mathfrak{g}$ (i.e., the largest solvable ideal in $\mathfrak{g}$) and by $\mathfrak{n}$ the largest ideal of $\mathfrak{g}$ composed only of nilpotent matrices. By Levi's theorem, $\mathfrak{g}$ is the direct sum of $\mathfrak{h}$ and of a semi-simple subalgebra $\mathfrak{f}$. It can be proved that $\mathfrak{h}$ is the direct sum of $\mathfrak{n}$ and of Abelian algebra $\mathfrak{a}$ whose matrices are semi-simple and commute with those of $\mathfrak{f}$.

Let $\mathfrak{g}$ be any subalgebra of $\mathfrak{gl}(n, K)$; then it can be shown that the derived algebra $\mathfrak{g}'$ is algebraic. Moreover, $\mathfrak{g}'$ can be "defined by its invariants," in the sense that any matrix which admits as its invariants all the common invariants of all matrices in $\mathfrak{g}'$ lies itself in $\mathfrak{g}'$. Our result applies in particular to any semi-simple Lie algebra $\mathfrak{g}$ of $\mathfrak{gl}(n, K)$, which is identical with its derived algebra $\mathfrak{g}'$. Moreover, our method of proof shows more generally that any subalgebra $\mathfrak{g}$ of $\mathfrak{gl}(n, K)$ whose radical is composed only of nilpotent matrices is algebraic and is defined by its invariants.

If A is any algebra (associative or not) over the field K, the derivations of A form a Lie algebra which is easily seen to be algebraic.

Finally, let it be mentioned that the notion of algebraic Lie algebras can be used with advantage in the exposition of the theory of semi-simple Lie algebras, notably in establishing Cartan's criterion of semi-simplicity and Lie's theorem on solvable Lie algebras. Barring the recourse to the algebraic closure of the basic field in the proof of Theorem 3 of the paper quoted above,[2] one obtains in this way a rational proof of Cartan's criterion and of Lie's theorem.

[1] Maurer, L., "Zur Theorie der continuerlichen, homogenen und linearen Gruppen," *Sitzungsber. d. Bayerischen Akad. Math. Phys. Classe*, **24**, 297–341 (1894).

[2] Chevalley, C., "A New Kind of Relationship between Matrices," *Amer. J. Math.*, **65**, 521–531 (1943).

TWO INTEGRAL EQUATIONS

By H. Bateman

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Let $k(s, t) = g(s, t) - c\, g(s, a - t)$ where $g(s, t)$ is a real continuous kernel for $0 \leq s, t \leq a$ and c is an arbitrary constant. The equations to be considered are

$$f(s) = \int_0^a k(s, t)\, F(t)dt \tag{1}$$

$$f(s) = F(s) - x\int_0^a k(s, t)F(t)dt \tag{2}$$

and the required function $F(t)$ is to be continuous when $f(s)$ is continuous. When this condition is supposed to be satisfied equation (1) may be written in the equivalent form

$$f(s) = \int_0^a g(s, t)[F(t) - c\,F(a - t)]dt$$

and when a continuous function $h(t)$ exists for which

$$f(s) = \int_0^a g(s, t)h(t)dt$$

a solution of the integral equation may be obtained by solving the functional equation

$$h(t) = F(t) - c\,F(a - t) \qquad 0 \leq t \leq a.$$

Since $h(a - t) = F(a - t) - c\,F(t)$ the solution should be

$$(1 - c^2)F(t) = h(t) + c.h(a - t).$$

If $c^2 = 1$ this last equation fails to determine $F(t)$ and this is just the case when the homogeneous integral equations

$$0 = \int_0^a k(s, t)E(t)dt, \qquad 0 = \int_0^a H(s)k(s, t)ds$$

have innumerable solutions. Thus, when $c = 1$ any solution of the functional equation $E(t) = E(a - t)$ which gives finite integrals is a solution of the first equation and if $L(t) = \int_0^a H(s)k(s, t)ds$, the second equation is satisfied whenever $L(t) = L(a - t)$.

For equation (2) the homogeneous integral equation

$$0 = E(s) - z \int_0^a k(s, t)E(t)dt$$

may be written in the form

$$E(s) = z \int_0^a g(s, t)[E(t) - c\,E(a - t)]dt \qquad 0 \leq s \leq a$$

Changing s into $a - s$ we have

$$c\,E(a - s) = cz \int_0^a g(a - s, t)[E(t) - c\,E(a - t)]dt$$

Hence the function $H(t) = E(t) - c\,E(a - t)$ is a solution of the quasi-adjoint[1] homogeneous integral equation

$$H(s) = z \int_0^a [g(s, t) - c\,g(a - s, t)]H(t)dt$$

When the equation for $E(t)$ is written in the form

$$E(s) - z \int_0^a g(s, t)E(t)dt + cz \int_0^a g(s, a - t)E(t)dt = 0$$

it is seen that

$$E(s) = -cz \int_0^a G(s, a - t)E(t)dt$$

where $G(s, t)$ is the solving kernel associated with $g(s, t)$. Now this is a

homogeneous integral equation for $E(t)$ and so $-cz$ is a root of the transcendental equation $\Delta(-cz, z) = 0$, where Δ is the determinantal function associated with the kernel $G(s, a - t)$ and is an entire function of $-cz$.

The kernel $k(s, t) = g(s, t) - c\,g(s, a - t)$ is only of a special type when $c^2 = 1$ for the two equations

$$k(s, t) = g(s, t) - c\,g(s, a - t),\ k(s, a - t) = g(s, a - t) - c\,g(s, t)$$

give the relation

$$k(s, t) + c\,k(s, a - t) = (1 - c^2)g(s, t)$$

from which the function $g(s, t)$ can be determined when c^2 is different from unity.

In the particular case in which

$$\begin{aligned} g(s, t) &= s(1 - t) \qquad s \leq t \qquad a = 1 \\ &= t(1 - s) \qquad t \leq s \end{aligned}$$

the integral equation (2) may be written in the form

$$f(s) = F(s) - x \int_0^1 g(s, t)[F(t) - c\,F(1 - t)]dt.$$

Differentiating twice with respect to s and using the known fact that $g(s, t)$ is the Green's function of the differential expression d^2y/ds^2 we obtain the two equations

$$f''(s) = F''(s) + x[F(s) - c\,F(1 - s)]$$

$$f''(1 - s) = F''(1 - s) + x[F(1 - s) - c\,F(s)].$$

Addition and subtraction gives the equations

$$f''(s) + f''(1 - s) = E''(s) + m^2E(s) \qquad m^2 = x(1 - c)$$

$$f''(s) - f''(1 - s) = B''(s) + n^2B(s) \qquad n^2 = x(1 + c)$$

$$E(s) = F(s) + F(1 - s), E(0) = E(1) = F(0) + F(1) = f(0) + f(1)$$

$$B(s) = F(s) - F(1 - s), B(0) = -B(1) = F(0) - F(1) = f(0) - f(1).$$

When $f(s) = 0$ we have simply

$$E''(s) + m^2E(s) = 0, E(0) = E(1) = 0$$

$$B''(s) + n^2B(s) = 0, B(0) = B(1) = 0.$$

Hence

$$E(s) = A \sin(ms) \text{ where } \sin(m) = 0, x(1 - c) = p^2\pi^2$$

$$B(s) = B \sin(ns) \text{ where } \sin(n) = 0, x(1 + c) = q^2\pi^2$$

where p and q are positive integers. The two equations

$$x(1 - c) = p^2\pi^2, x(1 + c) = q^2\pi^2$$

cannot generally be satisfied simultaneously although this can happen for special values of c. Usually when $x(1 - c) = p^2\pi^2$, $B = 0$ and when $x(1 + c) = q^2\pi^2$, $A = 0$.

In the general case in which $f(s)$ is not zero the solution of the integral equation (2) is

$$F(s) = f(s) + \frac{1}{2}\int_0^1 [U(s, t) + U(s, 1 - t) + V(s, t) - V(s, 1 - t)]f(t)dt$$

$$- \frac{1}{2}\int_0^s [m \sin \{m(s - t)\} + n \sin \{n(s - t)\}]f(t)dt$$

$$+ \frac{1}{2}\int_0^{1-s} [n \sin \{n(s - 1 + t)\} - m \sin \{m(s - 1 + t)\}]f(t)dt$$

where

$$U(s, t) = m \operatorname{cosec}(m) \sin(ms) \sin m(1 - t)$$

$$V(s, t) = n \operatorname{cosec}(n) \sin(ns) \sin n(1 - t).$$

Since

$$F(s) = f(s) + x\int_0^1 K(s, t)f(t)dt$$

where $K(s, t)$ is the solving kernel corresponding to $k(s, t)$, an expression for $K(s, t)$ may be written down.

The present example provides an interesting illustration of a method of solving a homogeneous integral equation of the first kind which was discussed about 36 years ago.[2]

When equation (2) with $f(s) = 0$ is written in the form

$$M(c)E(s) = \int_0^a [g(s, t) - c\, g(s, a - t)]E(t)dt$$

it seems likely that the values of c for which $M(c) = 0$ will be those for which the homogeneous integral equation

$$0 = \int_0^a [g(s, t) - c\, g(s, a - t)]E(t)dt$$

can be satisfied. Now in the present example the possible forms of $M(c)$ are

$$(1 - c)/p^2\pi^2 \quad \text{and} \quad (1 + c)/q^2\pi^2.$$

When $c = 1$ the function $\sin(ms)$ with an odd integral value of m/π satisfies the functional equation $E(t) = E(1 - t)$ and when $c = -1$ the function $\sin(ns)$ with an even value of n satisfies the functional equation

$E(t) = -E(1 - t)$. The known solutions of the homogeneous integral equation of the first kind are thus actually furnished by this method if it is agreed that a relevant solution of the functional equation $E(t) = \pm E(1 - t)$ can be expressed as a linear combination of the functions of type sin (mt).

[1] When $g(s, t) = g(t, s)$ the equation for $H(s)$ is adjoint to the equation for $E(s)$.

[2] H. Bateman, *Trans. Camb. Phil. Soc.*, **21**, 195 (1909); *Messenger Math.*, **39**, 6–19, 182–191 (1909–1910). Integral equations containing a parameter have been discussed also by G. Barba, *Relat. Soc. Gideniae Catinensis Nat. Soc. Catania*, **66**, 3–10 (1934); N. Gioranescu, *Bull. Sci. Math.*, s. 2, **58**, 270–272 (1934); *Rend. Semin. Mat. Padova*, **5**, 81–98 (1934); C. Miranda, *Palermo Rend.*, **60**, 286–304 (1937); R. Iglisch, *Math. Ann.*, **117**, 129–139 (1939).

VITAL STATISTICS OF THE NATIONAL ACADEMY OF SCIENCES

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Under the title "Vital Statistics of the National Academy of Sciences," Raymond Pearl, about twenty years ago when acting as Chairman of a Committee appointed to consider matters concerned with the rules for election to the Academy, published a series of articles which still deserve attention.[1] He gave figures for the mean and median ages and the standard deviation of the age distribution for different periods in the history of the Academy. I reproduce his results with the addition of those for the 81 persons elected in the three years 1943–1945, and with columns showing the percentage under 40 years of age when elected and the number elected in the period.

PERIOD	MEAN AGE	MEDIAN AGE	STANDARD DEVIATION	PER CENT UNDER 40	NUMBER ELECTED
Charter, 1863	51.7	51.3	11.1	16.7	48
1864–1883	44.5	41.3	10.2	45.5	95
1884–1904	46.5	45.1	8.5	20.0	65
1905–1924	50.5	49.5	8.1	8.4	213
1943–1945	52.1	51.8	7.6	3.7	81

It will be observed that the tendencies toward a higher mean age, a median nearer the mean, a smaller standard deviation about the mean, and a sharply decreasing percentage of really young persons elected, which Pearl so much deplored, have persisted and been intensified.

The average number of persons elected each year in the first twenty years after the charter was 4, in the next twenty years it was 3, in the twenty years 1905–1924 it was 11, and for the most recent three years it

was 27. At each time that there has been discussion of fixing the number who might well be elected each year, it has been held by some that the reason for the increasing average age at election was the increasing number of scientists of distinction who had not been elected to the Academy because of the small number who could be elected. There is no indication in the figures that the increased number elected has been sufficient to use up the accumulation of "older men who have not been elected"—if that is truly the reason for the increase in the mean age.

The first edition of *American Men of Science* in 1906 listed about 4000 whereas the seventh edition in 1944 listed 34,000. The number of members of the Academy in 1906 was 96 and in 1944 was 350. Whether the standard for inclusion in *American Men of Science* has declined or whether the fraction of really eminent scientists relative to the listings has declined would be difficult if not impossible to determine; but at any rate for each member of the Academy in 1906 there were about 42 persons in *American Men of Science* whereas for each Academician in 1944 there were about 97. The number of new starred names added to the volume in recent revisions has been at the average rate of 50 per annum.

Pearl computed a life-table for the membership of the Academy on the basis of the limited number (6273) of person-years of experience available from 1863 through 1924. A considerably larger experience is now available but for present purposes it will be satisfactory to use a standard life table.[2] The average expectation of life after election to the Academy as figured from this table and the age distribution of the 81 persons elected in 1943–1945 is 20.8 years whereas the expectation figured from the younger age distribution of 1864–1883 is 27.4, more than 30% higher. The ultimate size of the Academy if an average of 27 persons are elected each year, as during the past three years, on the basis of an average expectation of life of 20.8 years will be about 560.

It has long been known that annuitants have longer expectations of life than the insured. How closely to the 1937 Standard Annuity Table[3] the expectation of life of members of the Academy may prove to be when a sufficient experience has accumulated to give real stability to the results one cannot forecast, but it is interesting to note that from age 30 to age 70 the Annuity Table shows expectations of life about 2.4 years greater than those in the Standard Table Z based on insured lives, and would therefore give average expectations of life of 23.2 on the basis of the current age distribution at election, and of 29.8 on the basis of the age distribution of seventy years ago. Such increased expectations would mean proportionally increased numbers of members in the Academy if it elected a fixed number of persons annually until it reached a stationary population.

[1] These PROCEEDINGS, **11**, 752–768 (1925) and **12**, 258–261 (1926).

[2] After some discussion with Mr. Harold A. Grout, actuary of the John Hancock

Mutual Life Insurance Company, I have decided to use Table Z of the Mortality Tables and Life Insurance Statistics, which is an empirical table derived from the experience of insured lives, and which actually runs very close to the table Pearl computed for the Academy experience as of twenty years ago.

[3] The 1937 Standard Annuity Table, as well as the empirical Table Z, based on insured lives, was furnished to me by Mr. Grout, who informs me that the experience of the John Hancock Company with its male annuitants who purchased annuities from 1931 to 1943, inclusive, and who selected a non-refund type of annuity actually followed the table very closely.

AN AWARD TO THE ACADEMY

On April 19, 1945, the American Design Award for 1945, the diploma of which is herewith reproduced, was presented to the Academy and accepted by the President, Dr. F. B. Jewett, on behalf of the Academy, the

For the year
1945
Lord & Taylor
annual
American Design Award
Presented to
The National Academy of Sciences
in recognition of the Outstanding Achievements of the
Men of Science in the Prosecution of the War and for the
furtherance of Research for National Security

Research Council and all American science. The award carried a sum of $25,000 available to the Academy without restriction. The donors expressed informally the hope, however, that the Academy would find ways to employ the money for purposes which in its judgment seemed likely to enhance national security.

Although the award comes to the Academy as the officially recognized leader in the organization of science in the service of the Government, special mention was made of six members of the Academy who have been directing important scientific activities in connection with war research, namely Messrs. Vannevar Bush, J. B. Conant, K. T. Compton, R. G. Harrison, J. C. Hunsaker and Dr. A. N. Richards.

THE VARIATION OF INFECTIVITY, II

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We have discussed the variation of infectivity when certain curves are assumed as appropriate to describe the course of an epidemic.[1] One may also discuss the variation directly upon the data. Taking the infectivity as proportional to the reciprocal of the equilibrium value of m and using the law of mass action, we have

$$\text{infectivity} \propto \frac{1}{m} = \frac{1}{S}\left[\frac{C(t)}{C(t-\tau)}\right]^{1/\tau}. \qquad (1)$$

The ratio of the case rates one incubation period apart, when that is one-half the period used in the tabulation ($\tau = 1/2$), can be determined with adequate approximation[2] according to Soper as

$$\frac{C(t+1/4)}{C(t-1/4)} = \sqrt{\frac{K_0}{K_{-1}}}, \qquad (2)$$

where the K's represent the numbers of cases during the month after and before $t = 0$.

Proceeding with (1) and (2) applied to Hedrich's data for measles in Baltimore for 32 years we have found for each month the value of $1/m$. Owing to the irregularities in the course of epidemics the values for $1/m$ for the Januaries (or any other specified month) are highly variable. The means of the group of 32 are, however, reasonably stable with standard errors of estimate of about 5%. In table 1 the values of the means of k/m have been entered after choosing k so that the average in any row is 1.00—the values thus indicating a relative seasonal index of infectivity. A comparison of lines 1 and 8 in the table shows that the Baltimore index has a much larger variation than the one Soper derived for Glasgow from a smaller series of years (as adjusted by interpolation to 12 months instead of 13 four-week periods per year). To see whether the index for Baltimore

would vary greatly for different samples taken from the 32 years, we have tabulated in lines 3, 4, 5, 6, respectively, the index as computed from the 15 epidemic years (September through the following August) with the largest numbers of cases, the 16 epidemic years with the smallest number of cases,[3] the first 16 years, and the last 16 years. The largest years and smallest years seem surely to have different seasonal distributions of the index, but there seems to be no notable difference between the seasonal variation of the index in the first and second halves of the 32-year period.

The degree of variation in the index will clearly depend on the value chosen for p. The indices so far mentioned were computed for $p = 1$. If p be assumed to have the value 2, we have the results tabulated in line 7 of table 1 which show a smaller variation than those in line 1. In line 9 are given for six months[4] values of an index computed for the six clear-cut epidemics for which values of p have been determined from the relation of total cases to peak cases, the variation of $1/m$ in each being computed with the appropriate value of p; the constancy of the results is to be expected.

There are striking differences in the seasonal distribution of the incidence of measles in different places and for different sets of years. This seasonal variation is shown, in table 2, by the percentage of cases falling

TABLE 1

VALUES OF THE MONTHLY MEANS OF THE INFECTIVITY STANDARDIZED TO HAVE A MEAN OF 1.00 FOR DIFFERENT PERIODS FOR BALTIMORE AND FOR $p = 1$ UNLESS OTHERWISE SPECIFIED

MONTH	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.
Infect.[1]	0.79	1.10	1.46	1.25	1.26	1.17	1.12	1.05	0.95	0.73	0.60	0.53
(m)[2]	77	55	41	49	48	52	54	58	64	83	101	115
Infect.[3]	0.75	1.07	1.61	1.37	1.29	1.19	1.14	0.98	0.87	0.65	0.58	0.51
Infect.[4]	0.81	1.14	1.33	1.13	1.24	1.14	1.10	1.13	1.02	0.81	0.61	0.54
Infect.[5]	0.80	1.22	1.43	1.22	1.23	1.14	1.13	1.01	0.95	0.72	0.63	0.52
Infect.[6]	0.78	0.96	1.50	1.27	1.30	1.20	1.10	1.10	0.94	0.74	0.57	0.53
Infect.[7]	0.90	1.05	1.21	1.11	1.12	1.08	1.06	1.04	1.00	0.88	0.80	0.74
Infect.[8]	0.91	1.19	1.11	1.13	1.05	0.99	1.08	1.05	1.00	0.89	0.80	0.81
Intect.[9]	..	..	..	..	1.02	0.99	1.00	1.00	1.03	0.97	..	..

[1] Baltimore, 1900–1931. [2] Harmonic mean in thousands.
[3] Fifteen largest epidemic years. [4] Sixteen smallest epidemic years.
[5] Baltimore, 1900–1915. [6] Baltimore, 1916–1931.
[7] Baltimore, 1900–1931, $p = 2$. [8] Glasgow (Soper), 1905–1916.
[9] The six clear-cut Baltimore epidemics with p taken for each as determined.

TABLE 2

PERCENTAGE DISTRIBUTION OF MEASLES BY MONTHS

MONTH	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.
Balt.[1]	0.4	0.7	2.3	5.1	10.3	14.9	19.2	20.0	16.5	7.4	2.4	0.7
Balt.[2]	0.3	0.6	2.5	5.7	10.7	14.8	19.4	20.6	16.4	6.6	1.9	0.5
Balt.[3]	1.1	1.3	2.6	3.3	5.3	9.5	15.5	18.9	20.3	14.0	6.0	2.2
Balt.[4]	0.5	1.0	3.3	7.7	11.6	14.7	18.7	17.8	13.9	7.1	2.8	0.8
Balt.[5]	0.3	0.4	1.6	2.9	9.3	15.0	19.6	21.8	18.7	7.7	2.2	0.6
Glas.[6]	2.5	4.8	8.2	12.3	14.4	12.4	10.9	9.6	10.1	7.4	4.8	2.7

[1] Baltimore, 1900–1931. [2] Fifteen largest epidemic years.
[3] Sixteen smallest epidemic years. [4] Baltimore, 1900–1915.
[5] Baltimore, 1916–1931. [6] Glasgow, 1901–1916.

within the month. It will be seen from lines 2 and 3 that the seasonal distribution of cases differs in the largest and smallest years as was the case with the index of infectivity; however, here there is also considerable difference in the seasonal distribution of measles during the first and second halves of the 32-year period whereas there seemed to be nothing really significant in the differences of the seasonal variation of the index of infectivity. It may be noted that the seasonal variation of measles in Glasgow is quite different from that of any of the Baltimore series in that there is a long flat peak in December to February, instead of a sharp peak in March to April or April to May, and a relatively high incidence throughout the summer.

There is some indication in the data that the seasonal variation of the index of infectivity may be in some way related to the manner of variation of the seasonal distribution of the disease—as that the seasonal variation of infectivity is greater when the seasonal variation in the incidence is greater—but we would not wish to make such generalizations short of a more extended comparison of results in a variety of places or short of more intensive study of the details of the calculation. For example, we have spoken, following Soper, of the seasonal variation of the infectivity k/m. This variation may be largely due to the rise and fall of the epidemic which cannot be expected to follow perfectly any assigned law such as (1) and the seasonal variation of infectivity might therefore be largely due to the seasonal distribution of the disease. Indeed we saw that for $p = 2$ it was possible to get an exact solution of the equation, namely,

$$S = m\,[\cosh \alpha - \sinh \alpha \tanh \alpha t/\tau],$$

with m strictly constant; but if now we apply Soper's formula assuming $p = 1$, we have

$$\text{infectivity} \propto \cosh \alpha - \sinh \alpha \tanh \alpha t/\tau$$

and hence, as thus calculated, the infectivity would diminish throughout the epidemic from an initial value of $\cosh \alpha + \sinh \alpha$ to a final value of $\cosh \alpha - \sinh \alpha$, although actually $1/m$ was constant by hypothesis.[5]

We have assumed p as fixed and m or $1/m$ to be determined from month to month by (1) and (2); we may examine the question of determining both m and p from the monthly data. Indeed, we have from (1) and (2)

$$\log m + \frac{1}{2p} \log (K_0^1/K_{-1}^0) = \log S. \qquad (3)$$

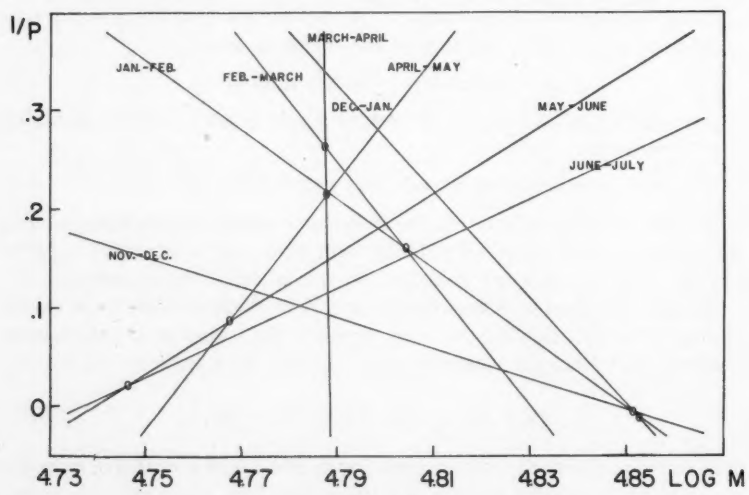
This imposes a linear condition upon $\log m$ and $1/p$ determinable from the cases in two successive months and the susceptibles a quarter of a month after the beginning of the second month. For the epidemic in Baltimore in the year 1912–1913, figure 1 gives the lines which result from the successive pairs of months. Owing to statistical fluctuations inevitable in

such phenomena as epidemics, the positions of the lines must be expected to show considerable instability. The intersections of successive pairs of lines determine the values of log m and $1/p$ that would be assigned in the different months of the year if we were to consider them both as variable, namely:

	DEC.	JAN.	FEB.	MAR.	APR.	MAY	JUNE
m	71,000	71,000	64,000	61,000	61,000	59,000	56,000
p	∞	∞	6.4	3.8	4.7	12	46

It is seen that m decreases (the infectivity increases) throughout the epidemic and that p decreases from very large values to a minimum of 3.8 near the peak of the epidemic and then increases to very large values. (Several of the epidemics of measles in Baltimore give similar results.[6]) There is certainly little evidence that p tends to be constant, although if one considered not only the intersections of successive pairs of lines but those of all the lines, there is some tendency of the intersections to cluster around the middle of the diagram near a point corresponding to the values $p = 4.3$, $m = 61{,}000$ appropriate to the relation between total cases and peak cases; there is no point of intersection which indicates a value of p so small as 1, or even 2.

The conclusion to be drawn from this behavior of p and m during the course of the epidemic, when both are regarded as variable, seems clearly



FIGURE

The lines $\log S = \log m + \frac{1}{2p} \log K_0^1 / K_{-1}^0$ determined from the cases in successive pairs of months in Baltimore 1912–1913.

to be that it is impracticable to consider the law of mass-action as accurately representing the dynamics of an epidemic with constant values of p and m, although for some purposes it may be a highly valuable approximation. As there is no observationally well-established value of p and as the *a priori* theory leading to the use of $p = 1$ is neither particularly convincing nor well suited to reproducing such a major statistical relationship as that between total cases and peak cases, as the computed variation of the infectivity (measured in terms of $1/m$) is so sensitive to the values,[7] fixed or variable, that may be used for p, and, finally, as the changes in the infectivity which may be due to the rise and fall of the epidemic cannot at present be separated from those due to the season as such, we infer that much further study will be required before one can have any confidence in the reality of the variation of infectivity that may be computed in some particular way from the data.

[1] These PROCEEDINGS, **31**, 142–147 (1945).

[2] If the case rate C is increasing (or decreasing) in geometrical progression as $C = ae^{bt}$, and if for symmetry we take C at $t + \tau/2$ and at $t - \tau/2$ and the cases K between t and $t + 2\tau$ and between $t - 2\tau$ and t we have $C(t + \tau/2) = ae^{bt}e^{b\tau/2}$, $C(t - \tau/2) = ae^{bt}e^{-b\tau/2}$ and

$$K_t^{t+2\tau} = \frac{a}{b}e^{bt}(e^{2b\tau} - 1), \quad K_{t-2\tau}^{t} = \frac{a}{b}e^{bt}(1 - e^{-bt});$$

the relation (2) is then exact. If the case rate be expanded in series,

$$C(t \pm \tau/2) = C(t) \pm \frac{\tau}{2}C'(t) + \frac{\tau^2}{8}C''(t) + \ldots,$$

$$K = 2\tau C(t) \pm 2\tau^2 C'(t) + \frac{4}{3}\tau^3\frac{C''}{2}(t) + \ldots,$$

$$\left[\frac{C(t-\tau/2)}{C(t+\tau/2)}\right]^2 = 1 - 2\frac{\tau C'(t)}{C(t)} + 2\tau^2\left[\frac{C'(t)}{C(t)}\right]^2 + \ldots, \quad \frac{K_t^{t-2\tau}}{K_{t-2\tau}^{t}} = 1 - 2\frac{\tau C'(t)}{C(t)} + 2\tau^2\left[\frac{C'(t)}{C(t)}\right]^2 + \ldots$$

and therefore the formula is good to terms in τ^2, inclusive, but inexact in the terms of order higher than τ^2 which involve higher powers of C'/C than the second and the derivatives of C or order higher than the first. As the interval τ can hardly be considered small for epidemics of measles, one may examine the accuracy of (2) for a variety of curves which may be fitted to the case rate and it appears that the formula involves a relatively small percentage error which can hardly be considered serious in view of the inevitable fluctuations in the course of observed epidemics.

[3] The point of division falls between two epidemics which had numbers of cases almost equal to the numbers of recruits during the year.

[4] The fluctuations outside the central range of epidemics are so great that for averages of only six no particular stability could be expected.

[5] The index of infectivity varies from $1 + \tanh\alpha$ to $1 - \tanh\alpha$ and with the values of α that may well arise in fitting the solution to an observed epidemic the variation may be of the order of magnitude shown in Table 1.

[6] If we write (1) as $\log m = \log S + p^{-1}(\log C_{-} - \log C)$ and differentiate with respect to the time to find the intersection of successive lines,

$$0 = \frac{1}{S}\frac{dS}{dt} - p^{-1}\left[d\frac{\log C}{dt} - \frac{d \log C}{dt}\Big|_{-}\right], \quad p = \frac{\tau d^2 \log C}{dt^2}\frac{S}{A - C}$$

where A is the rate of recruiting susceptibles to the population. Thus we should expect p to be infinite when $C = A$. The inflection points of log C would probably be well down in the trough of the seasonal curve. Thus we should expect p to be positive and near minimum at the peak of the epidemic, to increase to ∞ when $C = A$ either on the way up or on the way down, to be negative when C was between A and the presumably smaller values at which $d^2 \log C/dt^2$ becomes zero and to be positive between the two points in the trough where $d^2 \log C/dt^2 = 0$; but with actual data from an epidemic the instability due to fluctuations when $C < A$ would probably interfere with tracing the variation of the value of p. Figure 1, computed from finite differences, appears to check well enough with this general discussion based on differentiation.

[7] The values of k/m depend not only on those used for p; they depend on the general level of S and on the true number of cases (not the reported number) in so far as the variation in the value of S during the epidemic is concerned, but not in so far as the ratio K_0^1/K_{-1}^0 is concerned provided we may consider the proportion of cases reported to be constant during the epidemic. There are several hypotheses on which k/m may be computed: (1) The level of S is fixed and p is fixed but may have different values. This has been discussed above, using the level of S and the true number of cases as determined by Hedrich. (2) The value of p is fixed and unchanging but the level of S is unknown. It seems fairly clear that minor changes in the general level of S should not markedly change the variation of the index of infectivity k/m; but in some diseases on which one might wish to test the theory the general level of S might be unknown within fairly wide limits, and, as a matter of fact, some persons might differ fairly seriously with Hedrich's figures or with our conclusion that $5^1/_2$ years of recruits was a good estimate of the general level of S for measles in American cities. (3) As the statistical relation between total cases and peak cases and the theoretical expression for the period between epidemics depend effectively upon the ratio m/p rather than upon m and p severally, one might desire to discuss the changes in the "seasonal variation of infectivity" which would result from varying p and the general level m of susceptibles subject to the condition that m/p were constant. We believe that under this hypothesis the infectivity decreases throughout the major part of the epidemic but that the range of the index of infectivity diminishes as p increases.

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*STRAIN SPECIFICITY AND PRODUCTION OF ANTIBIOTIC SUBSTANCES. VI. STRAIN VARIATION AND PRODUCTION OF STREPTOTHRICIN BY ACTINOMYCES LAVENDULAE**

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Attention has already been directed[4, 10] to the fact that actinomycetes as a whole, and certain groups or species in particular, vary greatly in their cultural, physiological and morphological properties. The variable char-

acteristics include the nature and relative abundance of the aerial mycelium, the formation of various soluble and insoluble pigments, and the capacity of producing one or more antibiotic substances. These variations are obtained both for strains of presumably the same organism isolated from different substrates, and for variants of a single culture when grown on a variety of media and under different conditions. Moreover, the same culture frequently exhibits variations when grown on a certain medium for a considerable length of time. Some characteristic cultural or morphological properties may thus be gained or lost.

Schaal[8] reported that isolates of *Actinomyces scabies*, the causative agent of potato scab, produce variants that are culturally and morphologically different from the parent strains and from one another; they also differ in their pathogenicity upon potatoes. Some of these variants arise spontaneously, as previously demonstrated by Jensen[3] and others.[7] On the other hand, some investigators[2, 6, 11] have not accepted the concept of a fundamental change in the characteristics of the organism which would render it a distinct species; they believe that the variations are only temporary in nature and that the characteristics of the organisms remain constant provided cultural and environmental conditions are constant.

The phenomenon of variation among the actinomycetes has been a major cause of confusion in the nomenclature and classification of these organisms. A species once described on the basis of its cultural or morphological properties may not necessarily be recognized from the original description after several years of culture.[4] This may be particularly true of organisms isolated from different substrates and in different laboratories, especially if those organisms vary in some one cultural characteristic. The same species isolated by different workers has often been looked upon as representing a totally different oganism, especially when no sufficient recognition was given to the potential variability of the organisms. This fact often accounts for the different designations attached to the same species. An organism described by Müller,[5] in 1908, as *Actinomyces coelicolor* was later designated as *A. violaceus-ruber*,[12, 15] *A. tricolor* and *A. violaceus;* however, Conn,[1] in a study of the chemical nature of the pigment produced by different cultures of this organism, was led to suggest that one may be dealing, after all, with distinctly different species. The pigment as well may be a variable character.

Among the various actinomycetes belonging to the genus *Streptomyces*[17] formerly designated as *Actinomyces*, Waksman and Curtis[15] described, in 1916, an organism under the name of *A. lavendulae*. When freshly isolated, the culture of this organism was characterized by the production of a lavender-colored aerial mycelium on synthetic media and of a soluble brown pigment on protein media. This culture was not tested, when first isolated, for its capacity to form antibiotic substances, but when tested

recently, namely, after nearly 30 years in culture, it was found to show only weak antibiotic activity. This need not, of course, indicate that originally the culture may not have been an active producer of some antibiotic substance, since this property, as well, may have been either lost or largely reduced under conditions of artificial culture for this long period of time.

Since the first description of *A. lavendulae*, other strains of this organism or forms closely related to it have been isolated from the soil by the senior author and by various students and collaborators working in his laboratory.[16, 19, 13] Several strains were also received from other laboratories in this country. Many of these strains differed from the description of the original culture in some of the cultural characteristics, such as intensity or shade of pigmentation of the aerial mycelium and nature of soluble pigment when grown on organic media. However, these differences were considered to be only minor or quantitative in nature, and not of sufficient significance to justify the designation of any of the new strains as different species. This point of view seemed justified since the original culture itself underwent, during the long period of cultivation, marked changes in pigmentation, and abundance and nature of aerial mycelium.

Among the various isolations of *A. lavendulae* cultures in our laboratory, there was one that possessed† distinct antibiotic properties. The isolation of this culture happened to coincide with an intense interest in the laboratory[18] in the subject of antibiotic substances. On further study,[19] this culture proved to have the capacity of producing an active antibiotic agent which was designated as streptothricin. However, it was found to be rather variable in nature, as shown by the fact that a number of variants, differing in their capacity to produce streptothricin, could be readily isolated[13] from it. These variants were found, more recently, to differ also in certain other cultural and physiological characteristics, notably the production and nature of the soluble pigment, and the presence of aerial mycelium.

Experimental.—The degrees of cultural, physiological and morphological variation among different strains of *A. lavendulae* and of closely related forms can be illustrated even in a comparison of only several cultures. Among the physiological properties of the strains, emphasis was laid upon the production of the antibiotic substance streptothricin. These cultures are listed here under the various laboratory numbers.

No. 3330. The original strain of *A. lavendulae* which was isolated in 1915, and has since been maintained in the culture collection of the Department of Microbiology of the New Jersey Agricultural Experiment Station.

No. 3440-8. A strain of the active streptothricin-producing culture of *A. lavendulae*, isolated in 1941. Among many strains, this and the following one were selected for this study.

TABLE 1

CULTURAL AND MORPHOLOGICAL CHARACTERISTICS OF DIFFERENT STRAINS OF *A. lavendulae*

ORGANISM	NUTRIENT AGAR		GELATIN		MILK		POTATO PLUG			DEXTROSE ASPARAGINE AGAR
	AM[a]	SP	LIQ.	SP	COAGULATION	PIGMENT	AM	SP	AM	SPORULATING HYPHAE
A. lavendulae[b]	O	Br	+	O–Br	O	Br	O	Black	Lavender	Spirals and straight
No. 3330[c]	White	None	+++	O	O	Br	O	O	White	
No. 3440-8	O	Br	++	Br	O	Br	O	Black	Lavender to rose	Compact spirals
No. 3440-14	O	Br	++	Br	O	Br	O	Black	Lavender to rose	Straight
No. 3445	O	Br	+++	Br	O	Br	O	Black	Lavender to rose	Straight, some spirals
No. 3465	White	Br	+	Br	O	Br	O	Black	Lavender to rose	Compact spirals

[a] AM = aerial mycelium; SP = soluble pigment; Br = brown; Liq. = liquefaction.

[b] Based on original description of organisms.

[c] Original culture of *A. lavendulae*.

No. 3440-14. Another strain of the streptothricin-producing culture of *A. lavendulae*.

No. 3445. A culture isolated from the soil.

No. 3465. A culture isolated in our laboratory in 1943 from a washed agar plate with *Mycobacterium tuberculosis* as the source of nitrogen. It is active, as determined by the streak method, against gram-negative bacteria and certain mycobacteria, but not against the gram-positive bacteria. Culture filtrates obtained by growing the organism on different media have been found capable of inhibiting only certain mycobacteria.

A brief summary of the cultural and morphological characteristics of these strains is presented in table 1. For comparative purposes, some characteristics of *A. lavendulae* as reported in the original descriptions,[12] are also included. Strains 8 and 14, derived from the same parent culture (No. 3440), were identical in most of their cultural characteristics. They differed, however, in three important properties not reported in the table. Number 8 produced a brown diffusible pigment on glucose-peptone agar after 2 weeks, whereas No. 14 did not; the latter produced much more streptothricin than the former; No. 14 grew normally on different media, in a manner comparable to the original culture, whereas No. 8 produced after 24 hours, on glucose-peptone slants, a distinct blue diffusible pigment which gradually became brown on the second or third day of incubation.

The results of comparative studies on the production of an antibiotic

substance by the various cultures of *A. lavendulae*, grown under stationary and submerged conditions, are given in table 2. Strains No. 3330 and No. 3465 were completely inactive under these conditions, whereas the other three strains showed varying degrees of activity. The nature of the antibiotic action was of distinct interest. All strains were either completely or nearly inactive against *Bacillus mycoides;* they were all active against both *Escherichia coli* and *Proteus vulgaris*, as well as against *B. subtilis;* the activity against the last was always greater than against *E. coli*. These specific antibacterial properties tend to indicate that the antibiotic substances produced by the various strains is of the streptothricin type.[13, 19]

Certain interesting differences in the nature of the antibiotic activity of strains No. 3440-8 and No. 3440-14 on the one hand, and of strain No. 3445 on the other, are also to be noted. Whereas the antibiotic substance produced by the first two strains was alike in all respects, save a difference in quantitative production, the substance formed by No. 3445 showed also certain differences that may be qualitative in nature. First, this substance produced in stationary culture had limited action against *B. mycoides;* second, the ratio of the antibiotic activity against *B. subtilis* as compared to *E. coli* was usually wider for strain No. 3445. Further information, however, tends to indicate that possibly this difference in nature of the antibiotic substance produced by the two cultures may only be quantitative rather than qualitative, as brought out in table 3.

Strain No. 3440-8 was found to undergo considerable variation on further cultivation. Some of the variants obtained from this strain produced on glucose-peptone a blue diffusible pigment; others formed a brown pigment The variants producing blue pigment had a pale blue vegetative mycelium with scattered, small pin-point areas of deep blue. Upon complete sporulation, the vegetative growth was covered with thick lavender-colored aerial mycelium; occasional sunken areas were of a somewhat slightly bluish tinge, these areas corresponding to the pin-point regions of the deeper blue. The under surface of the vegetative growth was cream colored except for the small blue spots. The other variants produced a colorless to cream-colored vegetative growth free of any blue pigment whatsoever; one to two days later, a brown diffusible pigment appeared, the growth becoming covered with abundant lavender-colored mycelium. On subsequent transfer on fungus agar slants, the two types of variants proved to be rather stable.

Two distinct variants were thus obtained from strain 3440-8: (*a*) blue vegetative growth, a diffusible pigment which was initially blue, and lavender aerial mycelium of a slight blue tinge; (*b*) cream-colored vegetative growth, soluble brown pigment in peptone media, and lavender aerial mycelium. Two variants were also isolated from sectors of colonies of

TABLE 2

PRODUCTION OF AN ANTIBIOTIC SUBSTANCE BY DIFFERENT STRAINS OF *A. lavendula*

CULTURE NO.	DILUTION UNITS/ML. OF FILTRATE *E. coli*	*B. mycoides*	*Pr. vulgaris*	*B. subtilis*	CUP TEST, UNITS[a]
Shaken cultures, 2 days' incubation					
3330	0	0	0	0	0
3440-8	0	0	0	30	3
3440-14	75	0	50	100	22
3445	25	0	10	150	15
3465	0	0	0	0	0
Stationary cultures, 7 days' incubation					
3330	0	0	0	0	0
3440-8	0	0	10	75	7
3440-14	25	0	30	200	34
3445	25	10	30	300	24
3465	0	0	0	0	0

[a] Filtrates tested by cup method with *B. subtilis* as test organism.

TABLE 3

PRODUCTION OF AN ANTIBIOTIC SUBSTANCE BY *A. lavendulae* 3440-14 AND ACTINOMYCES 3445

Starch-Tryptone Medium, Shaken Culture Agar Streak Method, Activity Units

INCUBATION, DAYS	CULTURE NO.	*E. coli*	*B. mycoides*	*B. subtilis*	*S. aureus*	CUP METHOD, MM. ZONE
2	3440-14	50	<10	>300	50	33.5
2	3445	150	20	>300	150	31.0
3	3440-14	100	5	500	100	25.5
3	3445	100	20	750	150	25.5
4	3440-14	100	<10	300	75	..
4	3445	100	5	300	100	..

TABLE 4.

PRODUCTION OF STREPTOTHRICIN BY TWO STRAIN OF *A. lavendulae* AND TWO VARIANTS[a]

Shaken Cultures

CULTURE NO.	UNITS/ML. OF FILTRATE, AFTER DAYS 3	4	6
3440-8	38	25	26
3440-8 (*a*)[a]	<2	<2	Trace
3440-8 (*b*)[a]	64	50	42
3440-14	40	23	22
3440-14 (*a*)	23	23	..
3440-14 (*b*)	0	0	0

[a] (*a*) and (*b*) are variants obtained from strains Nos. 3440-8 and 3440-14.

culture 3440-14 grown on agar media; (*a*) white aerial mycelium, sometimes showing a faint shade of pink; and (*b*) devoid of aerial mycelium, except for a scant growth of sporulating aerial hyphae on some very old slants.

These four variants were compared with the original cultures No. 3440-8 and No. 3440-14, for their ability to produce streptothricin in shaken cultures. The results are presented in table 4. Strain 3440-8 was occasionally found to be less active than No. 3440-14. This may be due to

the fact that strain 3440-8 tends to separate into the two variants (*a*) and (*b*), the first of which is almost completely inactive, whereas the second is more active than the parent strain. In the case of No. 3440-14, however, the white sporulating variant (*a*) was active, although somewhat less so than the lavender parent strain; the (*b*) strain, free of aerial mycelium, was completely inactive.

In the case of strain 3440-14, therefore, the production of the antibiotic agent was associated with the ability of the culture to form aerial mycelium. This is similar to the results obtained in strain variation studies of *A. griseus*.[10] In the case of both organisms the variants which failed to produce aerial mycelium likewise produced inactive culture filtrates. This statement must apply, of course, only to the inactive asporogenous strains and their respective active parent cultures, since other independent isolations of both *A. griseus* and *A. lavendulae* have been found completely inactive in spite of the fact that they produced aerial mycelium.

Summary.—Different cultures of *A. lavendulae* differ greatly in their capacity to produce the antibiotic substance streptothricin.

Active cultures of *A. lavendulae* were found to give variants that differed morphologically, culturally and physiologically from the parent strain. Variants free of aerial mycelium did not produce any streptothricin.

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† This culture was isolated by Dr. W. Kocholaty, of the University of Pennsylvania, while working in our laboratory.

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